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THE EVOLUTION OF CRAYFISHES OF THE GENUS *ORCONECTES* SECTION *LIMOSUS*

(CRUSTACEA: DECOPODA)

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The earliest described crayfish species now included in the Section *limosus* of the Genus *Orconectes* was described by Samuel Constantine Rafinesque (1817: 42). He reported the species, which he named *Astacus limosus*, "in the muddy banks of the Delaware, near Philadelphia." How ironical it now seems, that when Rafinesque located at Transylvania three years later and traveled to Henderson, Kentucky, to visit a fellow naturalist, John J. Audubon, he could have collected from the streams of western Kentucky a crayfish that he might have identified as the species he had described from the Delaware. We now know that these streams of the knobstone and pennyroyal uplands are the home of parent stock of this group. Moreover, this parental population on the Cumberland Plateau is now separated from Rafinesque's *Orconectes limosus* of the Atlantic drainage by more than 500 miles of mountainous terrain. Even Rafinesque, with his flair for accuracy and vivid imagination, would have been taxed to explain this wide separation had he known it.

A decade after the death of Rafinesque, Dr. W. T. Craige received a blind crayfish from Mammoth Cave. An announcement of the new crayfish, identified as "*Astacus bartonii* (?)" appeared in the *Proceedings of the Academy of Natural Science of Philadelphia* (1842: 174-175). Within two years the impact of Dr. Craige's announcement was evidenced by numerous popular articles both here and abroad. Dr. Theodor A. Tellkamp, a German physician practicing in Cincinnati, published the first description of this cave species (1844a) and named it *Astacus pellucidus*.

It remained for Dr. John Sloan of New Albany, Indiana, to point out the place of the Group *limosus* of the midwest. Dr. Sloan's description and ecological notes were the basis of Bundy's description of *Orconectes sloani* (Bundy, in Forbes, 1876). Hay (1896) reluctantly described another species of the group, *Orconectes indianensis*, from southwestern Indiana, "which Dr. Faxon was at first inclined to regard [as] a variety" of *Orconectes limosus*. Cope (1871) who actually established and defined the Genus *Orconectes* introduced the name, *Orconectes inermis*, for the blind crayfish of southern Indiana caves, and this has remained a controversial designation (Rhoades, 1959). Faxon (1884) described *Orconectes harrisoni* from Irondale, Washington County, Missouri. It was later assigned to the Section *limosus* by Creaser (1934). I added *Orconectes pellucidus australis* (1941b) to the Section *limosus* from Alabama caves. *Orconectes rafinesquei*, *O. tricusps*, *O. pellucidus packardi* and *O. kentuckiensis* of the *limosus* Section were described in my paper on the crayfishes of Kentucky (1944). Hobbs (1948a, 1948b) has added to the Section *limosus* the *Orconectes wrighti* and *Orconectes shoupi* from the Cumberland drainage in Tennessee.

In this paper I have brought together the results of 25 years of collecting and research to explain the evolution, paleogeography, present distribution, and ecology of the 13 species and subspecies of the Section *limosus*.

METHODS AND MATERIALS OF INVESTIGATION

Field Collections

This study of North American crayfishes began in the summer of 1932. My paper on the distribution of *O. sloani* (1941a) was one result of 15 years of field work with the Ohio Division of Wildlife. While serving as a consultant with the Tennessee Valley Authority, I was able to collect, and have access to collections, from the southern Appalachians. Cooperative projects with the conservation departments of Kentucky and Indiana enabled me to make detailed surveys in those states. Collections covering a period from 1932 to 1960 include more than 16,000 records, mostly from eastern United States. The main part of the material is deposited with the United States National Museum. Other institutions and museums also hold significant parts of the collection. Personal holdings are limited to a small paratype and reference collection.

The manuscript collection for this period includes data sheets and field notes for all personal collections. Specimens were identified, the size of the collection noted, other biotic associates listed and all ecological data readily available at the time were included in the notes. From time to time research notes were organized from impressions resulting from field work and reading. A number of these are included in this paper. During the time this paper has been in preparation, stream conditions and ecology in ten of the states in which these species are distributed were studied.

Methods

The area over which the 13 species and subspecies, which constitute the Section *limosus* of *Orconectes*, are distributed includes parts of 15 states from the Atlantic Coast to Missouri and from southern New York to northern Alabama. Geographically speaking, these species occupy the coastal plain and ridge and valley region of the Atlantic states. In the midwest, they occupy the lower Ohio valley and Cumberland Plateau south to Mussel Shoals.

This study could not have been undertaken without many of the basic zoogeographical concepts of Ortmann (1902, 1905, 1906a, 1913, 1931). His pioneering work on the Allegheny divide and its role as a barrier to invertebrates laid the foundation for further paleogeographical studies on North American fresh-water faunae.

The glacial geology of the eastern states was a relatively new field in Ortmann's time. Ortmann himself was a contemporary of Newberry, Leverett, Taylor, Fairchild, Wright, and other well-known contributors to our knowledge of Quaternary geology. During the past 30 years a significant volume of new data has been collected in the glaciated area of the northern states which gives some indication of the condition of the pre-Pleistocene peneplain. Thornbury (1937) and Malott (1922) developed these data in Indiana. Stout (1938, 1943) and his coworkers have made many contributions to our knowledge of Ohio Quaternary geology. Jillson (1924), Twenhofel (1931), and Weller (1927) have made recent studies on Kentucky surface and cave geology. The most recent advance pertaining to this problem has been made by Wayne (1956) and Horberg (1950) in Indiana and Illinois. These workers used geophysical methods to determine the depth of the rock floors under those states. This buried surface and its sculpturing are indicative of the nature of Pliocene and Pleistocene physiography.

In this study, base maps of eastern United States with plastic overlays were used to illustrate glacial advances, distribution patterns, physiographic features

and other data. A series of such maps and overlays are included to make the sequence of Pleistocene changes more graphic. The figures with this paper illustrate certain salient stages in the survival and distribution of the crayfishes of the Section *limosus*.

These crayfishes are unknown as Pleistocene fossils. Consequently, any attempt to explain the occurrence and distribution of these 13 species and subspecies of *Orconectes*, either present or past, must be based upon a careful interpretation and intergration of geological, zoological, ecological, and geographical factors.

SYSTEMATIC REVIEW OF THE SECTION *LIMOSUS*

Phylum Arthropoda

Class Crustacea

Order Decapoda

Family Astacidae

Subfamily Cambarinae

Antennae long with a membranous scale. Antennules filamentous, of equal length, and with joints similar to those of the antennae. Antennular basopodite with spine. Epistoma large, flattened and excavated. Rami of gonopods of males more or less fused together with corneous tips slightly separated. Annulus ventralis of the female separated from the third thoracic sternite. Surface of the annulus denticulate or tuberculate. Body more cylindrical and appendages more slender than in the astacids. Gills on the basopodite of the fifth pair of pereopods absent, leaving only seventeen gills on each side. No folded membrane at the base of the external lobes of the gills (Hobbs, 1942).

A. Genus *Orconectes* Cope, 1871

First gonopod of the male, form I, biramous with slender acuminate tips. Third maxillipeds of normal size with a row of teeth along the inner margin of the ischiopodite. Hooks generally on the ischiopodites of the third walking legs and occasionally in the same location on the fourth walking legs.

B. Section *limosus* Ortmann, 1905

External genital appendages short, rather thick nearly to the tips and reaching the base of the third pair of walking legs. Tips separated for a short distance; each tip tapering to an acuminate point. Hooks on the third, or on the third and fourth, walking legs.

C. Group *rafinesquei* Rhoades, 1944

The short tips of the gonopods are recurved gently in the same direction.

1. *Orconectes harrisoni* (Faxon, 1884).—Rostrum broad with sides converging to small acute lateral spines. Cephalothorax somewhat depressed in region of cervical groove. Areola the width of three rows of punctae. Chelae heavy with double row of tubercles on the median margin of the palm; hooks on basal joints of third walking legs. Corneous tips of gonopods recurved and separated for a short distance. Inner tip markedly shorter than outer tip. Annulus ventralis with low anterior area and left sinuate ridge partially overlying a high area on the right.

This is a typical stream species confined to the small rocky streams in the St. Francois Mountains in Washington and St. Genevieve counties, Missouri.

2. *Orconectes rafinesquei* Rhoades, 1944.—Chelae rather heavy; hooks on the third walking legs stout and erect. Biramous parts of the gonopods straight except for the recurving tips. Annulus ventralis low with two widely spaced tubercles.

This species is limited to the Rough River drainage system in western Kentucky. The typical habitat is rocky or rubble bottom streams.

3. *Orconectes tricuspis* Rhoades, 1944.—Chelae decidedly more slender than those of other limosus species; hooks on the third walking legs blunt and depressed. Tips of the gonopods of the male, form I, recurved gently for most of their length with the curve accentuated in the tips. Annulus ventralis with two very high median tubercles.

This species is distributed in the lower Cumberland and upper Tradewater drainage in western Kentucky. These streams flow through the gravelly uplands. Crayfish dig pits under the larger stones or are concealed in the edges of *Justicia* beds.

4. *Orconectes shoupi* Hobbs, 1948.—Rostrum with lateral spines and lateral margins much thickened and concave. Areola nine to ten times as long as broad and 34 to 36 percent of the total length of the carapace. Chelae with long gaping fingers; hooks on the third walking legs only. Annulus spindle-shaped transversely.

This species occurs in tributaries of the Cumberland River in the Nashville area where rubble bottom and limestone ledges supply cover.

5. *Orconectes wrighti* Hobbs, 1948.—Rostrum bearing small lateral spines and with non-carinated surface heavily pubescent. Rostrum comprising 32 percent of carapace length and about six times as long as broad. Chelae moderately sculptured and the fingers costate yet the markings generally obscured by pubescence. Fingers not gaping. First pleopod of the form I male with tips sub-equal, separated for only a short distance and both slightly recurved. Annulus ventralis of the female sub-ovate. Central fossa flanked laterally by high tubercles. Sinus extending medially over high posterior rim.

This species was described from two localities in Hardin County, Tennessee, where hard clay and gravel formed a soft, sticky creek bed and the margins of the stream were set with emergent vegetation.

6. *Orconectes pellucidus pellucidus* (Tollkämpf, 1844).—Rostrum rather broad with sides noticeably converging. Lateral spines acute and upturned. Areola shorter and narrower than in the other *O. pellucidus* subspecies but quite variable in length. One, sometimes two, lateral spines on the carapace just posterior to the cervical groove. Chelae subcylindrical with many squamose tubercles on the inner margin of the palm. Pleopods of the form I male short with typically divergent tips. Annulus ventralis small and poorly sculptured with only a slight tendency toward convexity.

This blind white species has long been known from Mammoth Cave and is distributed widely in the solution caverns between the Cumberland River in central Tennessee and the counties of southern Indiana. Individuals are generally seen in the edges of clear stygian pools or hiding under rocks.

7. *Orconectes pellucidus inermis* Cope, 1871.—In establishing this new combination of names (Rhoades, 1959), I pointed out the following diagnostic characteristics: Lateral spines of the carapace reduced to blunt angles. Areola longer and slightly broader than in the Mammoth Cave specimens; chelae heavier and less spinous and tuberculate. Hooks on the third walking legs always present but variable; and hooks are absent from the fourth walking legs. Annulus ventralis greater in all dimensions than in Mammoth Cave *O. pellucidus* with the central prominence bulbous.

This is the blind crayfish of cave waters in Monroe, Brown and Bartholomew counties in south central Indiana.

8. *Orconectes pellucidus packardi* Rhoades, 1944.—This subspecies differs from the typical *O. pellucidus* from Mammoth Cave in having a shorter rostral acumen, a longer areola, more ovate antennal scale and more strongly recurved tips on the gonopods. Hooks are normally present on the ischiopodites of the third walking legs but are not always present on the fourth walking legs.

This blind subspecies occupies the cavernicolous drainage connecting with the

upper Cumberland River and South Fork in Pulaski and McCreary counties, Kentucky.

9. *Orconectes pellucidus australis* (Rhoades, 1941).—The armature of the carapace and chelae much reduced from that of typical *O. pellucidus*. Areola the longest of all the *O. pellucidus* subspecies. Hooks on the third walking legs only. Gonopods with very short tips and the outer ramus tends to clasp the inner ramus. Annulus ventralis with high hemispherical area close to the anterior margin.

This blind cave subspecies appears to be widely distributed and in considerable abundance in the large underground drainage of the Mussel Shoals region.

10. *Orconectes kentuckiensis* Rhoades, 1944.—Chelae slender with inflated palms and very long gaping fingers. Gonopods of the form I males with stout tips and with shorter inner ramus more strongly recurved than the outer. Annulus low and flat except for high central tubercular area on the posterior rim.

This species is limited to the Tradewater River drainage of western Kentucky. The decapod association in this muddy, low gradient stream is *O. kentuckiensis*, *O. immunis immunis*, *Cambarus diogenes* and *Palaeomonetes*. All occupy cavities under driftwood and trash or in *Justicia* beds.

CC. Group *limosus* Rhoades, 1944

Gonopods with short tips strongly divergent.

11. *Orconectes indianensis* (Hay, 1896).—Rostrum rather short and broad with slightly converging margins. Carapace with single lateral spine. Chelae slender, rounded, and smooth with no conspicuous markings on palm or fingers. Annulus ventralis low and slightly bituberculate anteriorly; posterior rim level with the fifth sternite.

Hay (1896) described the species from the Patoka River at Patoka, Indiana, and this remained the only record until I collected it from the Little Pigeon River and Anderson Creek in southwestern Indiana. The species is generally associated with accumulations of rubble or weed beds (*Justicia americana*).

12. *Orconectes sloani* (Bundy, 1876).—Rostrum long with straight, slightly converging margins. Lateral spines of the rostrum small or lacking. Broad short median carina. Lateral spines of the carapace acute. Areola wide (three to five punctures). Chelae keeled externally and marked by two rows of depressed tubercles of the inner margin of the palm. Copulatory appendages of the form I male short and thick; inner ramus recurving in a long gentle arc; outer corneous tip thicker and only slightly recurved. Annulus ventralis of the female with prominent divergent ridges parallel to the anterior margin, behind which is a deep narrow fossa walled posteriorly by a high central area.

This species is distributed principally on the Dearborn Uplands in southwestern Ohio and southeastern Indiana (Rhoades, 1941a). Streams of this area have generally trenched down to the thin courses of Ordovician limestone and shale. Loose accumulations of this material harbor an abundant *O. sloani* population. Where the species occurs in the Scottsboro Lowlands it is a limited burrower as originally described by Sloan (Hay, 1896).

13. *Orconectes limosus* (Rafinesque, 1817).—Rostrum long with subparallel sides elevated and with marginal spines well developed. Carapace finely punctate with a number of small spines on the hepatic region. Areola about 33 percent of the cephalothoracic length and rather broad, from 18 to 25 percent of its own length. Tips of form I male pleopods crossed and divergent. Annulus ventralis with anterior elevated area split by a median fissure. High posterior area giving the annulus a trituberculate appearance.

The species is restricted to the Atlantic drainage from the Connecticut River in New England to the James River in Virginia, but the metropolis of the species is in the freshwater affluents of Chesapeake Bay. Many studies of this species

indicate that it occupies vegetative cover areas or is associated with rubble. Rafinesque's original observations, made along the Delaware and dating from 1803, indicate that it is a burrower if other cover is absent.

OCCURRENCE OF PALEOZOIC AND MESOZOIC MALACOSTRACA

Arthropods generally, and Crustacea in particular, had reached a high level of development by the beginning of the Paleozoic era. The Subclass Malacostraca was represented by six genera found in the Burgess shale of British Columbia (Walcott, 1911). The lobster-like forms of the Eumalacostraca are commonly found in Maxon Creek concretions from the Pennsylvania rocks of Illinois. *Pseudopemphix*, the earliest known decapod, was a Triassic marine lobster (Roger, 1953). From this early beginning, the Order Decapoda swelled into prominence in the late Jurassic and early Cretaceous of central Europe. Forty species of *Homarus*, the heterochelid lobsters, were established on the shores of various continents by the end of Cretaceous time. Since then they have continually waned on the seacoasts of the world.

ASIAN ORIGIN OF FRESH-WATER CRAYFISHES (SUPERFAMILY ASTACOIDEA) IN CRETACEOUS TIME

The Superfamily Astacoidea, to which the fresh-water crayfishes of the world belong, had its origin in eastern Asia sometime before the close of the Mesozoic era (Ortmann, 1902). This was the time when the Herpochelida were at their height. It is plausible to consider a species of the homarid lobster complex to be a migrant into the fresh-water streams of the Angaran Shield of eastern Siberia. Roger (1953), in discussing the entrance of decapods into fresh water, points out that we cannot yet identify the original invader. He regards this ecological transposition, with subsequent morphological changes, as being monophyletic. Once a population were established, its dispersal would be dependent upon subsequent geological changes.

This development of fresh-water crayfishes occurred on the eve of the Laramide orogeny which closed the Mesozoic era with the elevation of the fringe of the Pacific basin according to Roger (1953). The Sino-Australian geanticline, which was a part of this elevation, closed the east end of the Tethys Sea and made the coast of the western Pacific continuous. The Asiatic fresh-water crayfishes crossed the equatorial belt on this connective in the temperate shadow of the western Pacific currents, cooled at that time by Arctic water flowing through a breach between Asia and North America. Once in the southern hemisphere, these Cretaceous parastacids migrated over land masses and connectives to most of the continents of the southern hemisphere. The present survivors of this first wave of migration are *Cheraps* in Australia, *Astacopsis* in eastern Australia, *Engaeus* in Tasmania, *Paranephros* in New Zealand, *Astacoides* in Madagascar and *Parastacus* in South America.

The Family Astacidae, on the other hand, appears to have been derived from an astacoid ancestor at a later date, possibly in the early Tertiary. By this time the old connectives over which the parastacids spread were gone, and there were new relationships between the circum-Pacific land masses. The strand of the western Pacific had become submergent and fractured into an archipelago. Another event of early Tertiary time was the eversion of the mid-Siberian trough which fused Europe and Asia into a continuous land mass. The genus *Astacus* appears to have had its origin in the Paleocene epoch in eastern China close to the present range of the astacid Genus *Cambaroides*. While this does not imply that *Cambaroides* is ancestral to *Astacus*, still, on the basis of simple bifid gonopods of the male and the lack of hooks on walking legs, characteristics which are regarded as primitive, *Cambaroides* is placed lower systematically than *Astacus*. Once derived, *Astacus* spread along the broad axis of the Eurasian land mass to Europe. Fossil astaci of undetermined species have been recorded from the

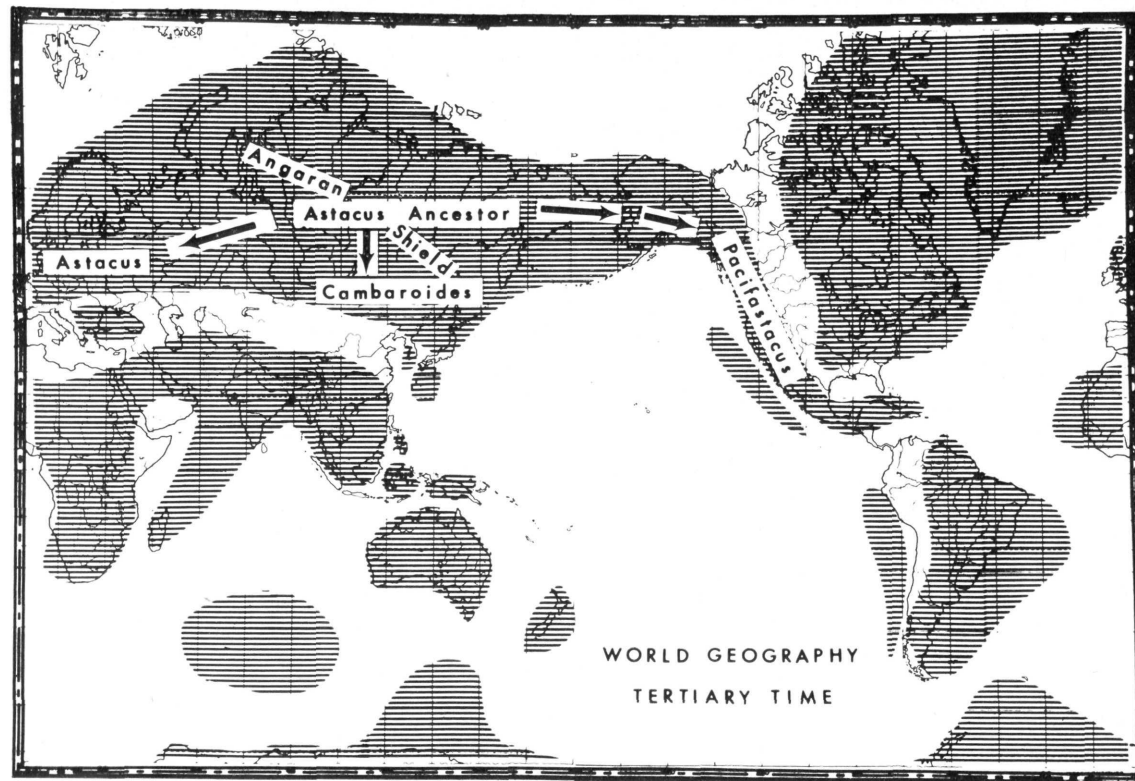


FIGURE 1. World geography in Tertiary time showing the distribution of fresh-water crayfishes. This map of early Tertiary geography shows the disappearance of the Volga Sea which closed the mid-Siberian trough and the thrust of the Ural Mountains. The Tethys Sea became continuous with the Pacific Ocean while a Bering land connective formed with the new cordillera of western North America. The Sundance seaway separated the North American Cordillera from eastern North America, and the Cordillera was continuous with the Antillean Continent. The origin, routes of dispersal, and distribution of the fresh-water crayfishes are shown.

Paleocene or lower Eocene of Germany. The genus is represented in Europe today by about ten species distributed from central Spain to Turkestan.

The Angaran Shield of eastern Siberia had been discontinuous from the North American land masses since late Triassic or early Jurassic (Flint, 1947). As a result, the earlier astacid derivants had been prevented from dispersing eastward to the nearctic area. The Laramide disturbance had everted the Cordilleran geosyncline in western North America producing a long, thin spur of mountains from Alaska to southern Mexico. Progressive uplift eventually connected this mountain chain with Asia. It was over this Bering Sea connective that the Asiatic astacid stock reached western North America (Ortmann, 1902).

The direction of dispersal of this fresh-water species could only correspond to the long axis of this narrow land so that, by the end of the Paleocene, the western North American land mass was probably populated by the Genus *Astacus*. Toward the end of the Laramide orogeny an area in the southwest, roughly corresponding to the Paleozoic continent of Llanoria, was re-elevated, breaking the continuity of the Cordilleran geosyncline and connecting the Cordilleran land mass with eastern North America. Likewise, it is thought that the supposed Antillean continent was connected with the North American land mass at the Yucatan or Florida tip or both. These changes extended well into Tertiary time (fig. 1).

MEXICAN ORIGIN OF THE SUBFAMILY CAMBARINAE IN TERTIARY TIME

During the pliothermic Eocene epoch the Sonoran and Chihuahuan areas of Mexico were well watered. Marine embayments and waterways deeply penetrated southwestern United States and northwestern Mexico. Brooks (1949) ventured to state that the Eocene climate of the region might have had a mean temperature of 68° F and an annual rainfall of 70 in.

Somewhere on the fringe of this area a mutant crayfish stock developed. The new characteristics varying from Astacidae were closer to those of the subfamily Cambarinae. They had larger and more specialized genitalia and a pleurobranchia in the last thoracic somite was lost (Ortmann, 1906a).

The main metropolis of *Astacus* was in the mountain streams of the new Cordillera which prevented a migration back along the mountain chain. The connective between Mexico and South America was broken in Oligocene time by severe peneplaning of the mountains from Alaska to central Chile. The new cambarid crayfishes could spread only eastward. Apparently, the first avenue of dispersal was the Yucatan-Antillean isthmus. The most primitive cambarids, the Genus *Cambarellus*, took this route to Cuba. *Cambarellus cubensis*, and *C. montezumae* are still distributed on both sides of the Yucatan channel which broke through the connective at the end of the Oligocene. Thus the Genus *Cambarellus* of the Subfamily Cambarinae must have been established at least before the end of Oligocene time. Other species of *Cambarellus* followed the streams of the aggrading lowlands around the Gulf of Mexico to the Mississippi embayment. This dispersal out of the center of origin was the result of numerous factors, one of which was the uplift of the Sierra Nevada and Sierra Madre Occidental which cast an orographic shadow upon the intermontaine plateau of the southwestern United States and central Mexico producing desert conditions. By the late Oligocene the cooling trend of the Tertiary period had set in. This aridity extirpated the populations that might have been intermediate between the Family Astacidae and the Subfamily Cambarinae.

Ortmann (1905) believed that the Genus *Procambarus* originated in the lowlands along the western Gulf Coast. This Genus, which most resembles *Cambarellus*, is represented by numerous species on the Gulf Coast and on the Atlantic Coastal Plain today. Fossil fragments of the cephalothorax of *Procambarus blandingii* forms have been recovered from Pliocene deposits of Alabama and Florida (fig. 2).

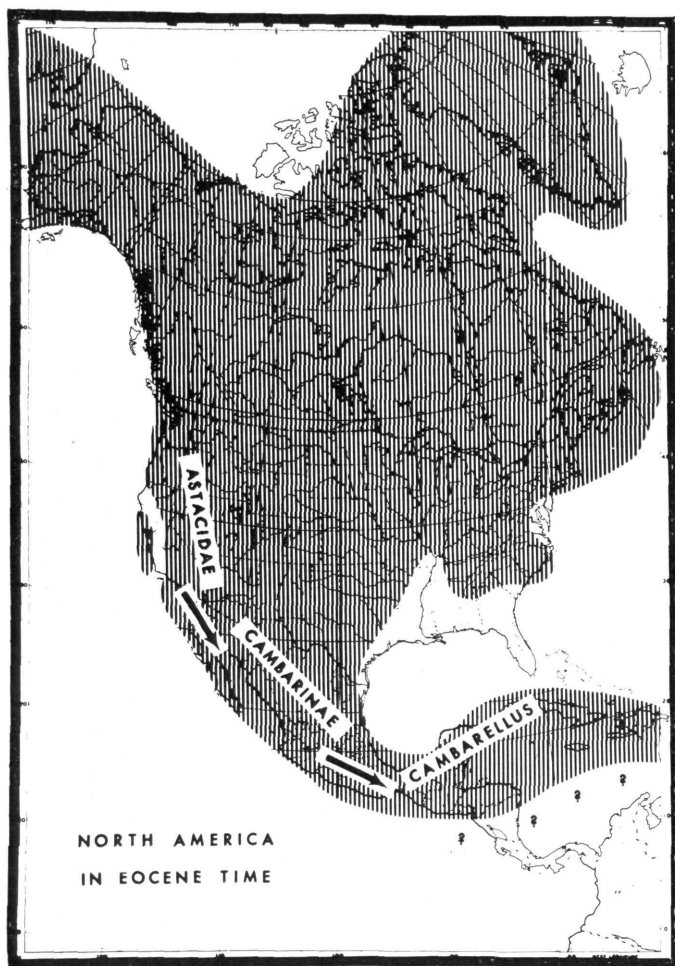


FIGURE 2. North America in Eocene time showing the distribution of fresh-water crayfishes. The Laramide orogeny in western United States had its inception movements on the western strand of the Sundance seaway. The closure of this portal came as a pinching action between the Kaibab Plateau and the Ozarkian Highlands, thus establishing the northwestern rim of the Gulf drainage in the Southwest. The early cambarids originated in this new area in new and unoccupied habitats conducive to the survival of mutant types. During Eocene time, the North American continent was still broadly connected with Asia. In the Central American region there was a connection with the old Antillean Continent, according to Schuchert and subsequent workers. This elevated region connected Yucatan with an area involving most of the Greater Antilles. It was over this connective that the Genus *Cambarellus* migrated to Cuba at least by early Oligocene time.

PROBABLE ORIGIN OF THE GENUS *ORCONECTES* IN THE OZARKIAN HIGHLANDS IN LATE MIOCENE TIME

Ortmann (1905) suggested that the center of origin of the Genus *Orconectes* was a broad area from the Ozarks to the foothills of the Cumberlands in Tennessee. This area is occupied today by a great complexity of local species whose systematics are only now being studied by Hobbs, Penn, and Williams.

In an attempt to restrict the area of origin of *Orconectes* we may consider the

genus as having originated from *Procambarus* stock as it spread into the high gradient streams of the hinterlands. Apparently, with no other cambarid species present, occupation, competition, and resulting selection pressure were at a minimum and small, mutant-bearing populations succeeded in becoming established. In light of the great size of the mid-Tertiary Mississippi embayment and its broad aggrading lowlands, which are not *Orconectes* habitat, the Cumberland Plateau may not have been occupied until much later. Moreover, the clinal tendency in specific evolution is from west to east around the embayment crescent as will be noted in dealing with the Section *limosus*. It would not be expected that the genus originated on the east side of the embayment and migrated westward becoming more primitive. Thus, it seems that the genus originated on the northwest

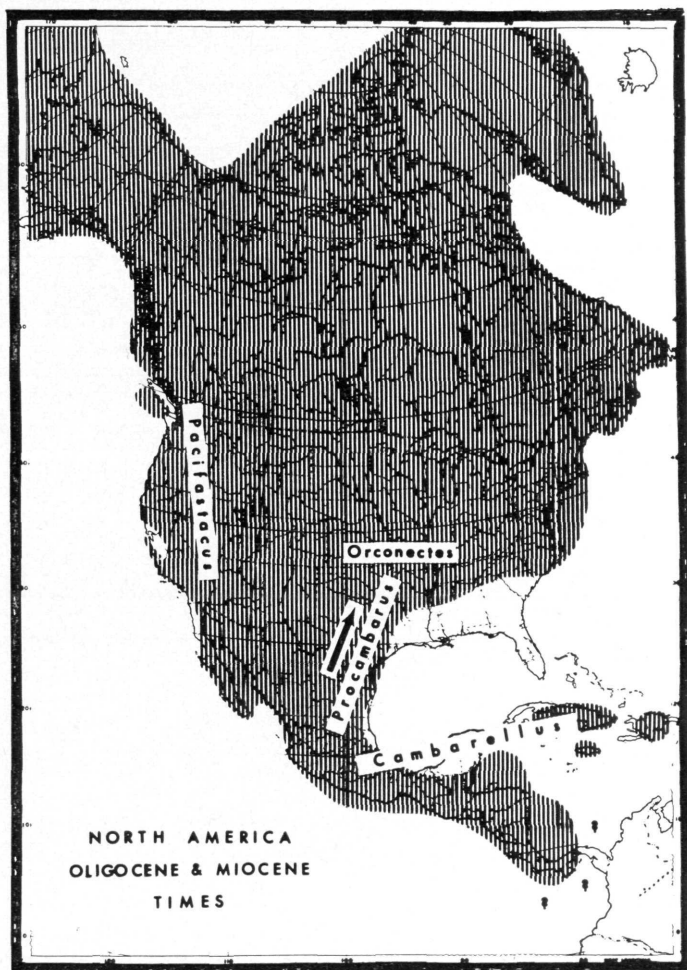


FIGURE 3. North American in Oligocene and Miocene times showing the distribution of fresh-water crayfishes. The connection between Yucatan and the West Indies was broken in Oligocene time giving the Gulf of Mexico and its coastal margin a more tropical climate. The Genus *Cambarellus* spread along the Gulf Coast to southern United States. *Procambarus* developed in the coastal lowlands. *Orconectes* developed in the Ozarks and on the Cumberland Plateau in late Miocene time.

flank of the Mississippi embayment particularly in the rocky streams of the Ozarkian Highlands. The Ozark Plateau of the mid-Tertiary was elevated somewhat higher than it is at present, and the physiographic character appears to have been only slightly different from what it is today. The area has been under peneplanation since Cretaceous time but land surfaces have remained high and streams have been rejuvenated by successive Tertiary uplifts more or less correlating with the re-elevation of the Cumberland and Appalachian areas (fig. 3).

CUMBERLAND ORIGIN OF THE SECTION *LIMOSUS* IN EARLY PLIOCENE TIME

Hard Mississippian and Devonian rocks form an almost continuous scarp from the Springfield Plateau of central Missouri through southern Illinois to western Kentucky. The streams on these uplands provided a continuous ecological corridor through which the late Miocene or early Pliocene species of *Orconectes* could have swept around the marshy lowlands and occupied the lower reaches of the Pliocene Teays and Ohio rivers.

These migrant populations became isolated into two groups on the basis of: 1) occupation of the Pliocene Teays River, the discharge of which poured into the head of the Mississippi embayment, and 2) continued migration along the escarpment streams to the Pliocene Ohio River. The isolated populations in these two major drainages subsequently developed genetic differences. The *Orconectes* on the Cumberland Plateau developed divergent tips on the gonopods which are now considered characteristic of the Group *rafinesquei*. Those *Orconectes* in the lower courses of the Pliocene Teays River developed recurved tips on the gonopods, and these are designated as belonging to the Group *limosus* (fig. 4).

PRE-KANSAN CONDITIONS AND KANSAN CHANGES

Physiographic Conditions

The Cumberland Plateau, on which the Group *rafinesquei* developed, was uplifted during the Appalachian orogeny. The most ancient features preserved on the plateau are remnants of the Cretaceous peneplain (Malott, 1922). After perfect peneplanation in the Mesozoic, the area was raised in the early Tertiary as the Lexington Peneplain, degraded somewhat, and re-elevated in late Tertiary time to a level of 800 ft (Davis, 1930; McFarlan, 1943).

The scores of papers published on pre-Pleistocene physiography of the Cumberland and Appalachian provinces generally agree on a sequence of events which modified the topography of the region. Remarkably few of these authors agree on the extent of modification. It is not the purpose of this paper to resolve all differences of opinion that have been expressed by authors on Tertiary geology and Pleistocene changes. Many of these opinions have been critically examined, and I have drawn conclusions which seem feasible in light of the present paleogeographic undertaking. The sequence of events which occurred in the Cumberland and Appalachian regions has been summarized by Stout and Lamb (1938: 49-50):

- (1) Monadnock hills and ridges, representing possible remnants of the original surface.
- (2) Harrisburg peneplain, the oldest well defined erosion surface.
 - A. Uplift and rejuvenation.
- (3) Lexington peneplain, best developed to the west.
 - B. Uplift and rejuvenation.
- (4) Parker strath with Teays, Pittsburgh and Dover drainage systems developed. [The entire preglacial drainage of the region had developed and was moderately entrenched.]
 - C. Flooding and filling of valleys through damming by early drift sheet, possibly Jerseyan.

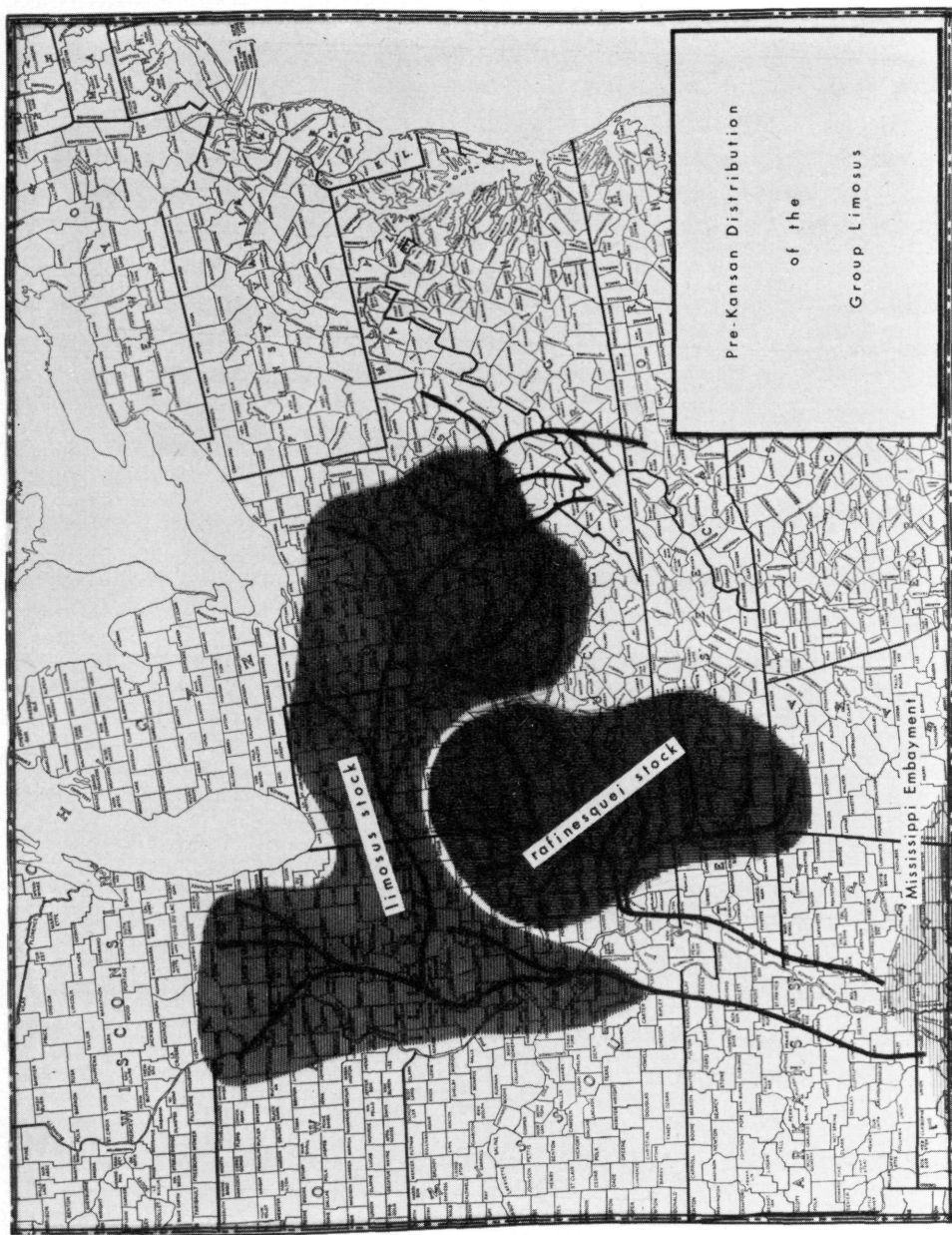


FIGURE 4. Pre-Kansan distribution of the Group *limosus*. The western portion of the Cumberland Plateau was drained by a short stream system occupying the area of the present lower Ohio Valley. The lower Ohio and Tennessee rivers joined at a point near Cairo and flowed to the Gulf in their own channel that hugged the bluffs along the western edge of the Cumberland Plateau. This is the stream bed of the present Yazoo River. This stream system, separate and distinct from the Teays River, was inhabited by the precursor species of the Group *rafinesquei*.

The drainage of the Cumberland Plateau and the heart of the southern Appalachians followed the master stream, the Teays River. This river system, in the main, was at least as old as the Cretaceous era and may be as old as the Triassic period. In Pliocene the *limosus* precursor occupied the Teays drainage and possibly the upper Mississippi. The possible barrier to further distribution eastward was the Flushing escarpment in eastern Ohio and central West Virginia.

The surface streams that drain the slopes of the plateau were short. This dendritic fan of small rivers had its rim on the back slope of the Silurian-Devonian escarpment on the western flank of the Cincinnati anticline and flowed through breaches in the Knobstone and Dripping Springs Escarpment. Enough of this drainage is undisturbed today to determine its extent in pre-Pleistocene time. The present Ohio River channel follows the Tertiary channel from the Falls of Ohio to Chain of Rocks, Illinois. The ancient drainage included the Vermilion and Saline rivers in Illinois, and the White, Patoka, Blue and Muscatatuck rivers in southern Indiana. In Kentucky it included Little River, the Tradewater, Green, Pond, Rough, Mud, Barren, Gasper, Nolin, Little Barren, and the Salt rivers. It was this drainage that harbored the *rafinesquei* stock in Pliocene time.

These rivers, according to Davis (1930), were consequent upon the contours of the Mesozoic plateau and degraded to old age as peneplanation advanced. After late Tertiary diastrophism, these rivers trenched into the topography but retained the characteristic meanders of their former maturity. The main stem of the Pliocene Ohio River passed along the Cache River valley in southern Illinois on a channel bottom about 100 ft lower than the present Ohio River bed. It then veered southward around the Cretaceous bluffs walling the embayment lowlands on the east and continued southward through western Kentucky, Tennessee and Mississippi in a channel now occupied by the Yazoo River.

Subsequent to the early Tertiary uplift and the entrenchment of the surface drainage, ground water began to expand crevices in the limestone brecciated by Permian thrusting and displacement. Rainfall, at least at times during the Tertiary, must have exceeded the rainfall on the area today (Martel, 1900; Matson, 1909) since most spelean streams under the Cumberland karst country are underfit. Geologists more or less agree on the important role played by carbonic acid in the solution along crevices. To explain the enormity of the Mammoth Cave labyrinths, however, it may be necessary to consider the role of sulphides and sulphates leached from the Mississippian overburden of the area. The reactions catalyzed only by carbonic acid have had the same time to perforate the Ordovician and Silurian limestones of the Blue Grass region, yet the caves are not extensive.

Once the rock fissures were enlarged sufficiently to direct a flow of ground water, then corrasive action accelerated the enlargement of the passageways. This concept implies that underground drainage is subsequent to surface drainage. Proctor (1898) believed the cave drainage of the Kentucky karst cut down at the same rate as the Green River. Essentially, then, the karst land drainage of the area from southern Indiana to northern Alabama beneath the Cumberland Plateau consists of merely the stygian tributaries of a dendritic stream system which has been developing since early Tertiary time. According to Weller (1927) cave levels are correlated with diastrophic displacement. Cave streams, like surface streams, wear down to base level, leaving channels and passages hanging high above the water table. In the vast labyrinth of Cumberland caves many high level caverns are now considered "dead" in that flowing water has ceased to have any formative effects.

Because of its historic significance, the Mammoth Cave system has been most attractive to cave geologists. Yet, cavernous limestones extend from south central Indiana to northern Alabama. The Alabama caves are noteworthy for their phenomenal effluents which apparently collect from vast subterranean channels under the Sand Mountains.

Group rafinesquei of the Cumberland Plateau

Antiquity of the group and the origin of blind cave crayfishes.—There can be little doubt that the Group *rafinesquei* has occupied the streams of the Cumberland Plateau since very ancient times. Perhaps the Pliocene surface species, that occupied the trenching streams, entered rock-fissure springs and lived in subterranean

water courses. The detailed mechanics of the atrophy of the eyes and the emphasis of tactile structures are beyond the scope of this paper. It may, however, be intriguing to consider briefly the interaction of cave environment and genetics.

Selection pressures to which surface crayfishes are subjected are very different from those of caves. In caves, weather has a minimum effect; predators are lacking. Light, which governs some motor reactions and rhythmic behavior, is absent. The eye, a high metabolic organ, would seem to have negative survival value in a habitat where food is so scarce. Cave crayfishes feed largely upon decayed wood and bat manure. Both of these items are devoid of Vitamin A and Vitamin B₁₂ which are regarded as essential in photoperception (Wright, 1939). It may be that crayfish living under cave conditions may not form the visual purple associated with the formation of optic images. As a consequence, crayfishes may have been physiologically blind before they become morphologically blind (Duke-Elder, 1958). Since the functioning eye continues to require energy difficult to obtain from the spelean environment, a crayfish bearing a genetic mutation which suppresses eye development has a distinct advantage over the eyed individuals. Since cave populations are always small, such a mutation could survive and the frequency of the mutant gene may be greatly increased by selection in a relatively short period of time. Individuals of the new type in which less calories of energy are required are no longer limited in the areas that they may occupy. They may penetrate deeply into caves beyond the hordes of bats or the influx of organic material through sink holes. This would serve to intensify isolation and contribute to greater homozygosity in the blind population. In the generosity of geological time could come the increase in tactile sense of the appendages, the expansion of the olfactory sense to all joints of the antennae and other cave adaptations by the integration of genetic mutations and environmental pressures.

Surface species on the Cumberland Plateau.—The surface *rafinesquei* complex on the Cumberland Plateau consists of six distinct species. *Orconectes rafinesquei* is known only from the Rough River drainage. *Orconectes kentuckiensis* is indigenous to the Tradewater River drainage. *Orconectes tricuspis* occurs in Little River drainage. *Orconectes shoupi* is endemic to the Cumberland drainage of the Nashville area. *Orconectes wrighti* is reported from the Tennessee drainage below Mussel Shoals. *Orconectes harrisoni* is confined to the rocky streams of the St. Francois Mountains in northeastern Missouri.

Dr. William J. Wayne, Glacial Geologist with the Indiana Geological Survey, expressed to me his belief that the entire expanse of Pleistocene time is required in most cases to derive a population bearing specific differences. He believes that all of post-Kansan time is required to produce subspecific changes particularly in Quarternary Mollusca. If Wayne's criterion were applied to the *rafinesquei* group on the Cumberland Plateau, it may be inferred that populations in the respective drainages have been isolated since Pliocene time. There is no question that these species are specifically distinct. The differences are so great that Hobbs (1948a) suggested other affinities among the species of the Section *limosus*.

The Cumberland Plateau Group *rafinesquei* generally do not occur with *Orconectes* associates. Perhaps their ancient occupation of certain drainages in numbers that were close to maximum for the production potential of the drainage, excluded other species as later waves of *Orconectes* migration swept over the area.

Orconectes harrisoni is the only species of this complex occurring west of the Mississippi River. It is confined to the high gradient headwaters of Big River in northeastern Missouri. Creaser (1934) in dealing with the species points out its general lack of affinities with other species. He noted that both tips of the gonopods are corneous which is a condition lacking in all other *Orconectes*. The tips are short and recurved in the same direction like those of the other species of the Section *limosus* Group *rafinesquei*.

In this characteristic *O. harrisoni* may be close to the limosus-precursor species of Pliocene time which populated the preglacial Teays and Ohio River drainages. It would be difficult to say whether the cornification of the inner tip is secondary upon the limosus gonopod type, or whether two corneous teeth represent a further development of a *Procambarus* type in which one of three terminal corneous teeth was lost by a series of changes in the genitalia. Creaser did not attempt to explain the presence of the species in Missouri. He did theorize that *O. medius*, indigenous to the upper Meramec River, is now sympatric with *O. harrisoni* in Big River because certain headwater tributaries of the Meramec drainage were pirated by headwaters of Big River.

It is my belief that *O. harrisoni* has occupied the headwaters of the Big River since Pliocene time when the limosus type of cambarid generally populated the Ozarkian and Cumberland plateaus. Upon the rise of the *O. rusticus* complex in the late Pliocene and its subsequent spread in post-Kansan time *O. harrisoni* and other early Pliocene species were reduced to relicts in small drainages. Severe Illinoian and Wisconsin aggradation in the lower reaches of the embayment rivers further isolated limosus populations in steeper headwater streams of the Ozarkian and Cumberland plateaus. These segments of a population have been separated since post-Kansan time by an unfavorable ecological situation populated by other cambarids. Consequently, all surface species of Section *limosus* on the plateaus have been relicts since the beginning of the Pleistocene.

Cave species under the Cumberland Plateau.—It would be difficult to say where rafinesquei stock first entered the subsurface drainage under the Cumberland Plateau. It appears that a specific population of *Orconectes pellucidus* was established and was widely distributed in the labyrinth of Cumberland caves by the beginning of Pleistocene time. Perhaps their wide distribution occurred in the late Pliocene when cave corrosion was at its deepest stage and all channels were free from filling. Isolation, which was a factor in subspeciation of *O. pellucidus*, came about as a function of river entrenchment and subsequent aggradation. While the Ohio River flowed upon a channel bottom scoured in the cavernous Mitchell limestone in the Fort Knox area during the immediate pre-Pleistocene, blind crayfish might presumably emerge from passageways opening in the river bottom on the south side of the river and enter other passageways beneath the opposite bank. With glacial filling of the river channel and sedimentation in the interrupted end of cave tunnels, especially in Illinoian time, a barrier was formed which isolated a population north of the Ohio River. This fraction of blind crayfishes north of the Ohio River is still heterogeneous with respect to its lack of armature which is diagnostic of *Orconectes pellucidus inermis* of Mayfield Cave. Most of the blind crayfishes from southern Indiana counties still possess the spinosity and other features of the Kentucky *O. pellucidus*. This may be the result of late Pleistocene isolation. It may also be that relatively uninterrupted passageways lie under the Ohio River permitting a limited contact between the northern Kentucky *O. pellucidus* and those of southern Indiana.

Similar entrenchment and sedimentation in the upper Cumberland River could lead to the separation of a segment of *O. pellucidus* in the caves of southeastern Kentucky, and this population is now designated *Orconectes pellucidus packardii*. The blind *Orconectes* in the subterranean channels of the Mussel Shoals region were similarly isolated and have been described as *Orconectes pellucidus australis*. The surface streams have been at least partial barriers to aquatic cave animals.

Group limosus of the Lower Teays Valley

General physiography.—The Teays River, the master stream of the eastern interior drainage of Tertiary time, had its source east of the Blue Ridge escarpment in Virginia and the Carolinas. It passed northward along the edge of the

Piedmont, breached the Blue Ridge, meandered northwestward across West Virginia and Ohio and turned westward and southwestward across Indiana and Illinois. Its 800 mile course lay in a watershed of some 200,000 square miles.

Dozens of papers, particularly those of Leverett and Horberg in Illinois, Wayne and Thornbury of Indiana, Stout, Ver Steeg, and Lamb of Ohio, Janssen and Tight of West Virginia make the preglacial Teays valley and its features as familiar as a modern river. Its valley, prior to glaciation, had a width in West Virginia and southern Ohio of about 1.5 miles. In Illinois it was 5 miles wide, and before it emptied into the Gulf embayment it was 15 miles wide. From elevations of rock floors it is clear that the main stream had an average gradient of about 7 in. per mile, which is about the gradient of the lower Mississippi today. From these data it is possible to reconstruct an ecological picture of this ancient river before it was choked by the wasting walls of the Kansan ice sheet. It was a mature stream with few tributaries to its lower reaches. In this respect it is like the present Missouri River. The heavily dendritic part of the drainage lay in southeastern Ohio and West Virginia between the elevated Lexington Peneplain and the Flushing escarpment in eastern Ohio. Following the elevation of the peneplain the Teays and its tributaries cut down and produced river terraces. The features of these deepened channels, with secondary peneplanation partially complete are referred to as the Parker Strath and represent conditions at the close of the Pliocene epoch in the area.

The Group limosus.—From our knowledge of the ecology of the group today, we believe that the precursor species invaded the drainage from the embayment area to the flat top ridges of eastern Ohio and the scarp walls of the Blue Ridge. This occupation occurred over a considerable period of time. The limosus crayfish in the Teays River differed from the rafinesquei crayfish on the Cumberland Plateau by having divergent tips on the gonopods. The species *Orconectes indianensis*, *Orconectes sloani* and *Orconectes limosus* exhibit this characteristic. These are the species of the Group *limosus* of the Section *limosus* of the Genus *Orconectes*.

Changes Resulting from Kansan Ice Invasion

As the continental ice spread over the Paleozoic rocks of the midcontinent, drainages were disrupted by tongues of dirty ice and gravel trains formed under excessive loads of debris and meltwater. Later, this was overrun by ice, and gravelly clay was rubbed into the unevenness of the landscape. Even the mighty Teays did not have enough corrasive action to keep the channel across Ohio, Indiana, and Illinois open. A lake, referred to as Lake Tight (Bownocker, 1899), was impounded to a height of 780 ft above sea level. The Warren River of Stout and Lamb (1938), draining the eastern tier of counties in Ohio south to Monroe County, as well as adjacent parts of West Virginia and Pennsylvania, was also dammed by the ice. The Bellaire River, a southwest tributary of the Warren River, was flooded until it broke down a col between its source and the source of the Marietta, a major eastern tributary of the pre-Kansan Teays River. This added discharge of water caused Lake Tight to flood over a col between a western tributary of the Teays and a tributary of the Cincinnati River. The Cincinnati River was also impounded by Kansan ice and in turn this ponded water broke down a col west of the Kentucky River and spilled into the unglaciated basin of the Tertiary Ohio River (Leverett, 1930). Thus, the Pleistocene Ohio River developed by the connection of marginal lakes. Leverett (1930) believes that the general absence of Kansan valley trains, benches, or terraces on the Ohio River is due to the enlargement of the drainage as well as the isostatic rebound occurring in post-Kansan time.

The extent of Kansan glaciation is debatable. Glacial boulders of northeastern Kentucky assigned a Kansan age may be the result of rafting by icebergs.

Stout, Ver Steeg and Lamb (1943) believed the Kansan ice actually invaded northern Kentucky covering the Licking valley. This would have caused the Kentucky River to carry the meltwater waste of the terminal edge. Leverett (1930) stated that the contour of the Kentucky River channel bottom indicates that the river never bore such a discharge. It is well established that the Kansan ice formed a re-entrant about the Mitchell Plains and Crawford Uplands in southern Indiana. Moreover, the southern tip of Illinois remained unglaciated.

Survival of Limosus Stock in Kansan Time

The invasion of Kansan ice separated the Teays limosus population into three segments.

One segment survived east of the terminal moraine in southeastern Ohio and northeastern Kentucky. The former drainage in this area included streams in the basin of extinct Lake Tight and the dispersed elements of the old Teays headwaters. In Yarmouth time, the new Ohio River completely traversed the plateau. This river was the route by which limosus crayfish penetrated the Appalachian highlands to the very brink of the older Appalachians. Since the rusticus, propinquus and cambarus lines had not yet invaded the area, *O. limosus* was the only crayfish inhabitant of this sprawling drainage.

West of the debatable Kentucky lobe, in the southern Indiana re-entrant, crayfish forced out of the ice covered central Teays valley followed sluiceways into headwaters of the White and Muscatatuck rivers and survived the Kansan glaciation behind the Knobstone Escarpment. This population led to the formation of *Orconectes sloani*.

A third segment forced through glacial sluiceways between the flooded tributaries of the central Teays and the lower Wabash survived in small streams in the Sullivan Lowlands of southwestern Indiana. These became the population now designated as *Orconectes indianensis* (fig. 5).

Survival of Group rafinesquei of the Cumberland Plateau in Kansan Time

Since all of western Kentucky and the cave region of southern Indiana remained unglaciated, the Group *rafinesquei* generally remained in areas occupied during Pliocene time. Valley filling resulting from Kansan ice was only slight, and few areas were rendered untenable due to habitat changes. It is interesting to note that displaced populations of the limosus group actually came to overlie *O. pelucidus inermis*, the blind cave crayfish of southern Indiana, a member of the Group *rafinesquei* of the Cumberland Plateau.

Post-Kansan Distribution Patterns

The surface as well as the cave species of the Cumberland Plateau were isolated by ecological changes resulting from alluviation of the deep stream beds of the lower Ohio. This also opened the way for further extension of the range of *Procambarus blandingi acutus* and *Orconectes immunis* which are inhabitants of low-gradient bayous.

The newly-formed Ohio River, whose gradient was reduced in the lower reaches by aggradation and in the mid-section by isostatic depression, was an avenue of migration over which the younger *Orconectes propinquus* stock from the Ozarkian area migrated eastward into the remnant of the old Teays valley in eastern Ohio. *Orconectes propinquus* is a species of comparatively low-gradient streams. When a migratory segment of this population reached the underfit and upset drainage consequential upon the preglacial Teays drainage of southeastern Ohio and adjacent parts of Kentucky and West Virginia, it became established to the extent of replacing *O. limosus*. However, *O. limosus* did persist in the rocky streams of the Appalachian rim to the end of Yarmouth time.

O. sloani spread out upon the southern Scottsboro Lowlands and Muscatatuck Slope as the country recovered from Kansan ice. However, the Ohio River is a large stream and is not the habitat usually occupied by the Group *limosus*. As it was already populated by *O. propinquus*, *O. sloani* was then, and has been since, confined to southern Indiana and southwestern Ohio north of the Ohio River. There are no established records for *O. sloani* in the Ohio River or in the adjacent counties of Kentucky.

Orconectes indianensis may have spread during Yarmouth time through much of the Wabash drainage. It was probably the dominant crayfish of pre-Illinoian time in the White River from which the modern relict population has survived.

ILLINOIAN SHIFTS AND SANGAMON DISPERSAL OF CRAYFISH POPULATIONS

Orconectes limosus

The Illinoian ice flowed down over the Silurian and Ordovician plains of western Ohio. It came to rest in a crevassed waste which irregularly filled the valley of the Ohio River from Manchester, Ohio, to the Falls of the Ohio at Louisville, Kentucky. This impounded the Ohio, as the Kansan ice had dammed the Pliocene Teays River, and initiated a reversed drainage in the upper Ohio Valley which Stout and Lamb (1938) termed the New Martinsville River (fig. 6). These authors are not specific on the course of this river beyond the western limits of Pennsylvania. Did it continue northeastward through the St. Lawrence or the Mohawk valleys, or was that route also sealed off by the ice edge? Could it have cascaded through gaps in the Allegheny Divide and plunged into the Susquehanna, the Juniata, or the Potomac? The latter proposal seems to have the most merit since *Orconectes limosus*, the headwater species of the Yarmouth Ohio River, is now distributed throughout the Susquehanna drainage and the drainage of Chesapeake Bay. There may have been several competitive sluiceways which dumped

EXPLANATION OF FIGURE 5

FIGURE 5. Kansan glaciation and drainage changes. The Kansan glacier invaded the Teays valley and broke up the Teays drainage. The Ohio River was formed from parts of old drainages. The upper Ohio was originally a tributary to the Pliocene Erigan River; itself a part of the preglacial Laurentian System Lawrence. The central section of the Ohio was made up of tributaries of the Teays, and the lower Ohio followed channels of the old Cumberland Plateau drainage.

This modification in drainage resulted in widespread impoundment in front of the glacier. The level of the Lake Tight has been set at from 860 to 900 ft. As a result of outwash and trenching the new Ohio carried great loads of sediment. The upper Mississippi River was undergoing the same type of degradation. This resulted in rapid aggradation in the Mississippi lowlands below Cairo and the two rivers were thrown into a common channel extending to the edge of the Gulf at Vicksburg.

As the Teays drainage was broken up so was the great range of *limosus* crayfishes. The lower Teays country along the unglaciated Mississippi valley, the streams of unglaciated southern Illinois and the post-Kansan Wabash River were populated by a segment of *limosus* stock. With the return of pliothermic conditions this segment evolved toward an *O. indianensis* stock.

The section of the *limosus* stock inhabiting the Pliocene Cincinnati River and the Cincinnati Uplands was forced westward through sluiceways nicked into the Knobstone scarp by the Muscatatuck River. After surviving in the unglaciated re-entrant of southern Indiana, the population spread eastward in post-Kansan times to occupy the gently sloping west-facing flank of the Niagaran scarp in southeastern Indiana. The species probably did not occupy a very wide area for the Muscatatuck drainage was bounded on the east and south by the unbeveled lip of the Niagaran limestones. Had the species reached Laugherty Creek or the Ohio River, *O. sloani* would be represented today in the crayfish fauna of Kentucky.

The segment of the *limosus* population remaining in the old Teays valley in southeastern Ohio spread eastward beyond the Flushing escarpment after Kansan filling had softened the topography. This *limosus* stock not only crossed the Flushing escarpment but also became widely established in the upper Ohio River and tributaries during the post-Kansan.

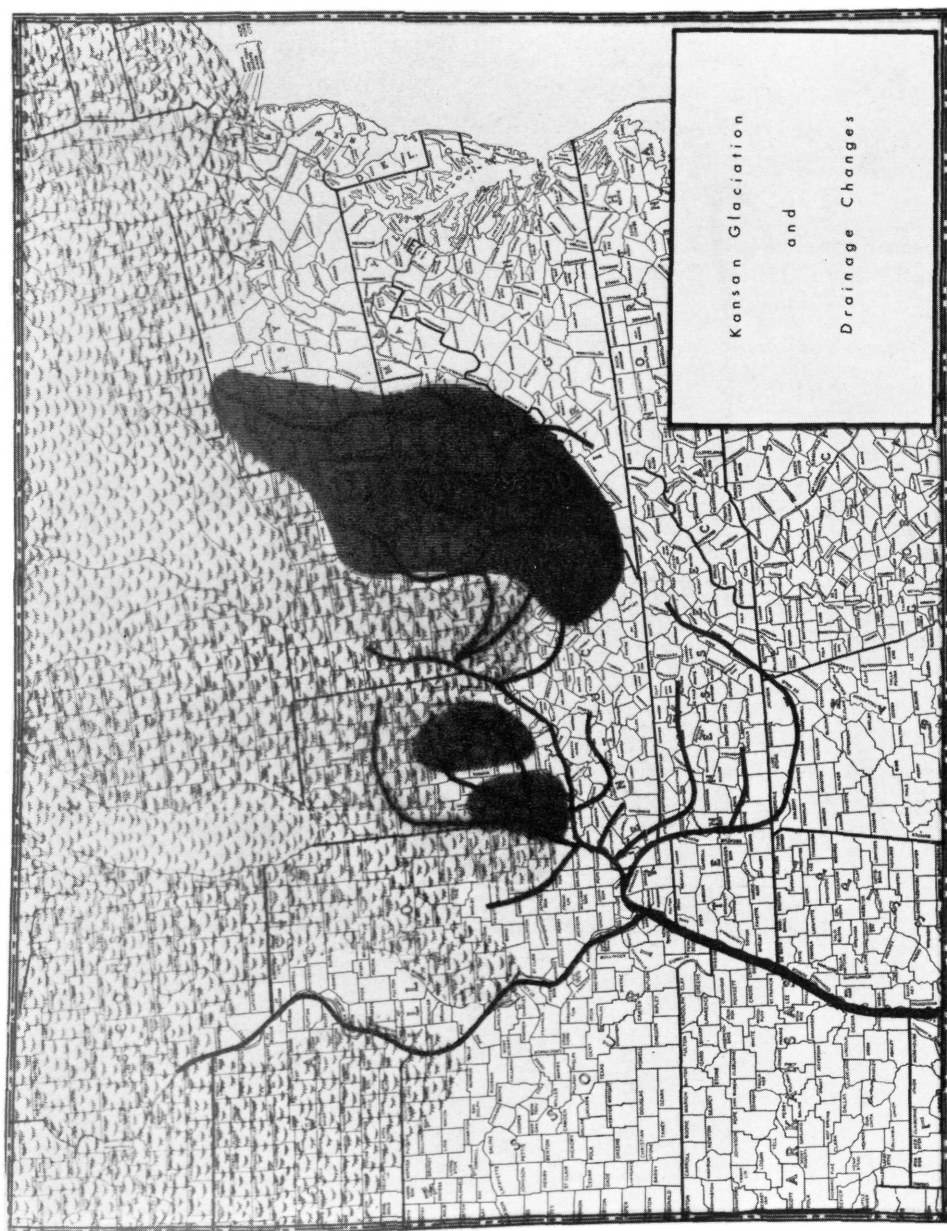


FIGURE 5

water and the fauna of middle America into the Atlantic Drainage. There may have been sluiceways between the headwaters of the Conemaugh and the Juniata in southcentral Pennsylvania. It is possible that the well-known piracy valley of Laugherty Creek may have been a sluiceway into Wills Creek and the Potomac. These direct routes of migration to the Atlantic drainage are favored because: (1) they were ice free at a time when this migration possibly occurred; (2) these gaps in the Allegheny strike may have been lower than at present, as indicated by gradation in the Potomac gravels during mid-Pleistocene; (3) the great similarity between the *O. limosus* of the eastern drainage and the Group *limosus* of the midwest indicates a rapid spread of a very large population. Were this migration to have occurred over a long route of varying ecological situations, clinal tendencies might be expected in the population. This has not been indicated by students of eastern crayfishes. The relict nature of the population of *O. limosus* in the inland drainage resulted from increased populations and distribution of *O. propinquus*. The Sangamon subspeciation to *O. propinquus sanborni* and new ecological tolerances in the subspecies of the upper Ohio Valley brought this population into successful competition with *O. limosus* even in headwater streams and extirpated *O. limosus* west of the Allegheny Divide. It is now apparent that *O. propinquus sanborni* actually followed *O. limosus* through the sluiceway gaps of the central Alleghenies into the Potomac.

Orconectes sloani

Orconectes sloani, apparently reduced to a remnant in the Muscatatuck drainage behind the Knobstone Escarpment of southern Indiana, re-invaded much of its former range. Leverett (1930) believed that the ice that flanked the Indiana re-entrant three times never stood very high, as indicated by lack of any vigorous drainage in the area. However, I believe that the mid-section of the Sangamon Ohio River, relatively de-faunated by Illinoian ice, became populated by *Orconectes rusticus*. This species had a pre-Pleistocene origin on the embayment arc, and had spread eastward over the Cumberland Plateau in Sangamon time. It then began to work northward along rocky limestone streams on the crest of the Cincinnati anticline. Sangamon invasion of the Ordovician and Silurian plains north of the Ohio River brought *O. rusticus* into close contact with *O. sloani* and restricted *O. sloani* probably even more than it had been restricted in post-Kansan

EXPLANATION OF FIGURE 6

FIGURE 6. Illinoian glaciation and drainage changes. During the maximum advance of the Illinoian glacier, the Ohio River was dammed at Cincinnati and the upper Ohio was again impounded. Stout and Lamb (1938) studying rock elevations and river terraces concluded that this part of the Ohio River flowed eastward in Illinoian time. During the fullest extension of Illinoian ice the old drainage channels to the sea through the St. Lawrence were under a considerable thickness of ice. Thus, sluiceways developed between the old Steubenville River (now the Allegheny) and the Susquehanna River where they lie parallel in valleys in northwestern Pennsylvania and between branches of the Youghiogheny and Cassel rivers and Wills Creek to the Potomac.

The *limosus* stock in the New Martinsville River that flowed eastward from the Cincinnati area was carried over the divide through these sluiceways. Once within the Susquehanna the species easily spread through these sprawling drainages to the Chesapeake Bay lowlands.

The Wabash River was under Illinoian ice as far south as its junction with the White River. Drainage changes on the ice front included the formation of three marginal lakes whose effluents carved the Patoka valley. *O. indianensis*, cut off by terminal moraines from becoming re-established northward, persisted in Patoka River and in Little Pigeon River and Anderson Creek, the Illinoian sluiceways of the Patoka River.

The central section where *O. sloani* had developed was covered with Illinoian ice to the very foot of the Knobstone Escarpment. *O. sloani* survived the Illinoian ice in the section of the Muscatatuck River west of the Knobstone Escarpment. As cold melt waters ceased to flow in this channel and warmer waters cut out the valley train the *O. sloani* moved eastward into the southern part of the Scottsboro Lowlands and across the Dearborn Uplands.

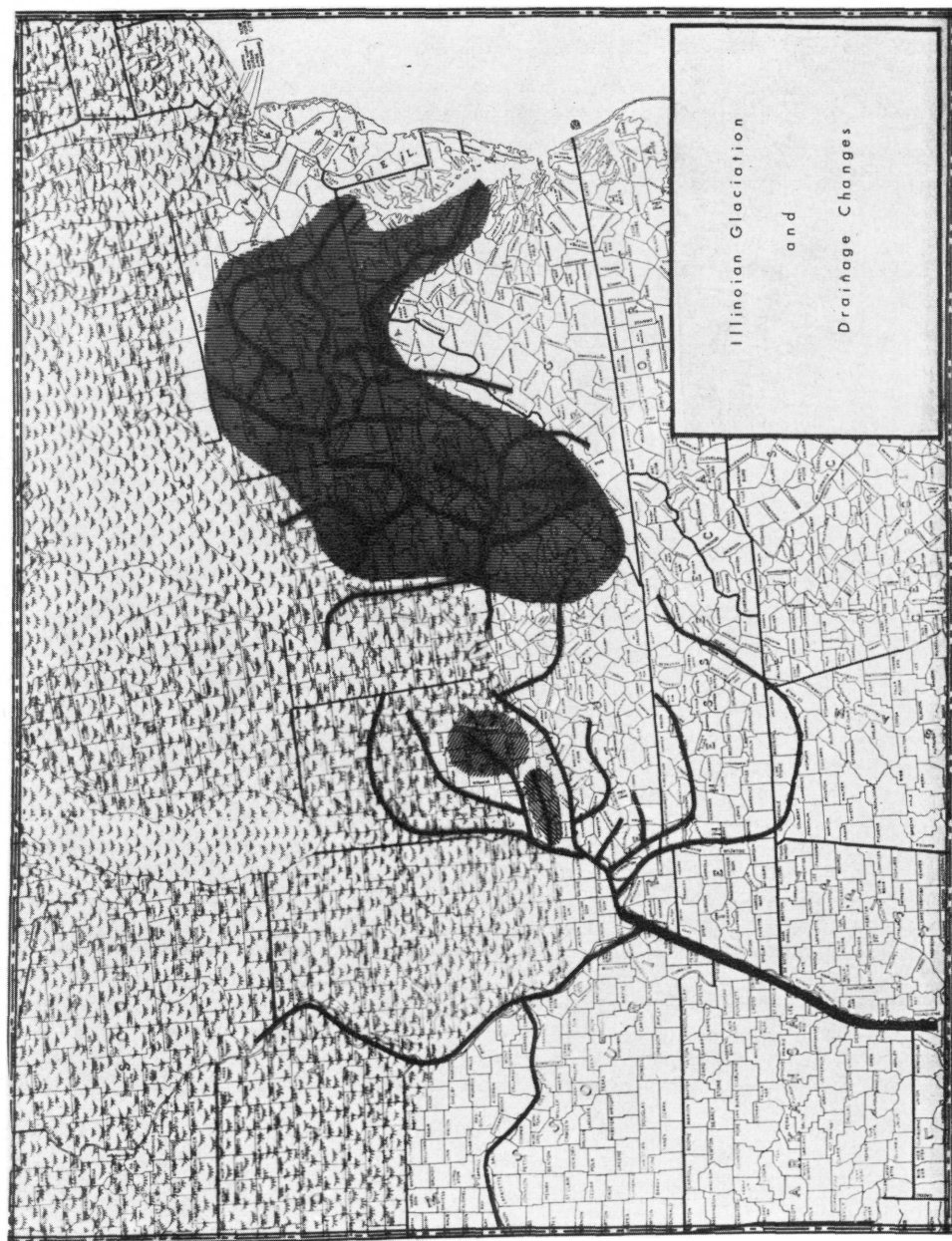


FIGURE 6

time. *Orconectes sloani* was probably confined to the Dearborn Uplands and kept relict within the bounds of this province by large streams such as the Ohio, Miami and White rivers.

Orconectes indianensis

This species which had populated a considerable range in the Yarmouth Wabash valley was pushed out by the Illinoian ice. This ice, heavily charged with detrital material from renewed plucking of lake basins and scouring of once glaciated and well-weathered till plains, dumped its debris in the lower Wabash. Leverett (1930) states that more than 1,000 square miles of lower Wabash country is aggraded to the depth of nearly 100 ft, making a total of nearly 20 cubic miles of glacio-alluvial material. This highly motile substratum, responding to torrents of cold water thick with glacial sludge, limited further the territory in which *O. indianensis* could survive the Illinoian ice invasion.

Prior to the Illinoian, three streams of moderate size flowed northward across southwestern Indiana. These emptied into the White River, an eastern tributary of the Wabash (Thornbury, 1937). The farthest advance of ice filled the lower White River valley and dammed these three streams with a terminal moraine. As a consequence, three marginal lakes developed. These acted as holding basins for the *O. indianensis* stock. At their height, these lakes had sluices into Anderson Creek and Little Pigeon River to the south which received a stock of *O. indianensis* at the climax of Illinoian glaciation. Effluents which reduced cols close to the moraine connected these lakes and developed the Patoka River. This peculiar river, reaching two thirds of the way across the state of Indiana, has a valley 35 to 50 miles wide. The Patoka drainage has remained the chief range of this species since Sangamon time.

The Cumberland Plateau Species

With the Ohio River interrupted by ice between Manchester, Ohio, and Louisville, Kentucky, there was no significant discharge of water westward through the valley in Illinoian time. The greatest wasting on the eastern continental ice front seemed to be on the flanks of the Illinoian lobe. As the valley floors of the lower Ohio and Wabash alluviated to a depth of nearly 125 ft, sedimentation in the Green, Tradewater, and other plateau streams from the south lagged behind. These rivers were ponded by the heavy train in the main Ohio Valley and lakes were formed. These valleys today are broad flat palustrine areas underlain by varved accumulation of alluvial and lacustrine clays, silts, and sands. This, as we have indicated before, is not the type of habitat occupied by Group *rafinesquei*. This heavy aggradation served further to limit and isolate the *O. rafinesquei* relicts on the plateau. At the same time the habitat required by *P. blandingi acutus* and *O. immunis* was extended.

The populations of hypogeal species under the plateau were not significantly influenced by the events of Illinoian glaciation.

WISCONSIN FAUNAL CHANGES AND RECENT DISTRIBUTION PATTERNS

No major distributional changes seem to have occurred in the Group *rafinesquei* beneath the Cumberland Plateau since Sangamon time. The surface species of this complex are isolated in small drainages and are surrounded by widely distributed species. The cave species occupy a habitat invaded by few other cambarids. *Cambarus bartoni tenebrosus* Hay, (1902) and *Cambarus cahnii* Rhoades, (1941) are small-eyed species living in Cumberland caves. Other surface cambarids frequently enter cave waters but are not typically associated with the spelean habitat.

Even the limosus group of species north and east of the Ohio River were relatively unaffected by Wisconsin ice.

Orconectes indianensis in its Illinoian-imposed range in southwestern Indiana was 80 miles south of the Wisconsin ice. *O. sloani*, that had occupied the Scottsboro Lowlands and the Dearborn Uplands in Sangamon time, was restricted somewhat in its distribution as a lobe of the Wisconsin ice flowed into the Miami valley. However, the unglaciated lower courses of Laugherty Creek, the White-water River and the Big Miami River could have harbored *O. sloani* during the maximum ice invasion of the Wisconsin. These served as a reservoir from which the upper courses of these streams could be repopulated as the ice retreated.

Orconectes limosus, which arrived in the Atlantic drainage at the height of Illinoian glaciation, became widely distributed in the Chesapeake Bay drainage in Sangamon time. Dispersal of this species into the Delaware drainage and the lower Hudson Valley may be a function of Wisconsin glaciation. The streams along the ice edge were impounded, diverted and pirated under unprecedented discharges of water. Francois (1959) pointed out that *O. limosus* is rare or absent on the sandy coastal plains in southern New Jersey. In light of these data, it appears that the species did not use the sandy tidewater route in its spread north-eastward. Rather, its route of migration is to be found in the higher-contoured, lake-studded area of northeastern Pennsylvania and northwestern New Jersey. *O. limosus* has invaded the lower Hudson valley south of Lake Champlain, as well as the Delaware and Susquehanna drainage north of the Wisconsin glacial boundary (fig. 7).

PRESENT DISTRIBUTION AND ECOLOGY OF THE GROUP *RAFINESQUEI*

1. *Orconectes harrisoni* (Faxon, 1884).

County Records: *Missouri*—St. Genevieve and Washington counties.

Faxon (1884) gave an adequate description of the species from Irondale, Washington County, Missouri, but said nothing concerning its ecology. Creaser (1934) indicates 14 localities in the Big River drainage. This area is in the St. Francois Mountains of southeastern Missouri about thirty miles west of the Mississippi River. It is a region of severely eroded Precambrian rock. Streams have a moderately high gradient, and there have been several local drainage changes. Creaser explained the presence of *Orconectes medius*, a member of the Group *rusticus*, in the Big River drainage by possible stream capture. Tributaries of the Big River undercut headwater tributaries of the Meramec River thus throwing *O. medius* and *O. harrisoni* into association. *Orconectes harrisoni*, apparently a rare pre-Pleistocene relict, is said to have no unique ecological characteristics. Creaser (1934) says "Concerning this species . . . practically nothing can be said." Williams (1954a) says "This species has no peculiar habits," yet he listed *O. hylas*, *O. punctimanus*, *O. luteus*, *O. medius* and *Cambarus hubbsi* as associates of *O. harrisoni*. It is unusual to have this number of species associated with a limosid crayfish. When a limosid crayfish and another *Orconectes* occur in the same stream, we may expect subtle differences in their ecological requirements that reduce the competitive tension between them. Rock and boulder stream bottoms would have numerous microecological situations which might permit two or more species to coexist.

2. *Orconectes rafinesquei* Rhoades, 1944.

County Records: *Kentucky*—Breckenridge and Grayson counties.

Orconectes rafinesquei is endemic to the Rough River drainage in west central Kentucky. The Rough River rises in the Dripping Springs escarpment, flows westward over the Mississippian shales and sandstones and empties into the Green River. In the headwaters and at Falls of Rough, bed rock and loose rubble provide an abundance of cover. Frequent beds of *Justicia* and *Potamogeton* are occupied by the smaller crayfish. Where rubble is absent and the bed of the

lower river is sandy, *O. rafinesquei* burrows in sandy banks bound down by willow roots. However, within a short distance *O. rafinesquei* is replaced by *O. immunis*.

3. *Orconectes tricusps* Rhoades, 1944.

County Records: *Kentucky*—Christian, Lyon, and Trigg counties.

This crayfish inhabits the Tradewater River drainage yet is found in Little River, a tributary to the Cumberland. It is highly probable that a Pleistocene connection between these two rivers across low drainage rims permitted the species to migrate from one to the other.

Typical of the other rafinesquei crayfish, *O. tricusps* is a species of gravelly upland streams with some rubble as cover. It frequently burrows when cover requirements are not otherwise met. Copulation was observed at Pete Light's Spring, 3 miles east of Canton, Trigg County, Kentucky, on September 4, 1941. A female with eggs was collected in the head of the Tradewater River 4 miles north of Hopkinsville, Christian County, Kentucky, on May 14, 1941.

4. *Orconectes shoupi* Hobbs, 1948.

County Records: *Tennessee*—Davidson County.

Orconectes shoupi has a limited distribution in Mill Creek and tributaries just south of Nashville, Tennessee. Hobbs (1948a) mentions five localities in this small drainage which is a tributary to the Cumberland River. In describing the type locality he states that the creek flows over sand and rubble and that there are limestone ledges in the headwaters of Mill Creek. In its life history the species seems to follow the pattern of other *Orconectes* in that form I males molt and emerge as form II males in July. Shoup collected immatures in July.

5. *Orconectes wrighti* Hobbs, 1948.

County Records: *Tennessee*—Hardin County.

Hobbs reported this species from two localities in Hardin County, Tennessee, a few miles from the southern Tennessee state line and on the west side of Pickwick Lake. This may be a very local relict since I do not recall seeing it in several hundred records from the Mussel Shoals area. In all, Wright's collections included eleven specimens. This is probably the southernmost surface species of the

EXPLANATION OF FIGURE 7

FIGURE 7. Wisconsin glaciation and recent distribution of the surface species of the Group *limosus*. *O. indianensis*.—This species was relatively undisturbed by the Wisconsin glacier. It had already been restricted to the Patoka River and its Illinoian sluiceways southward to the Ohio.

O. sloani.—*O. sloani* survived the Kansan and Illinoian glaciers in the Muscatatuck River and tributaries in unglaciated southern Indiana west of the Knobstone Escarpment. In Wisconsin time the southern part of the Scottsboro Lowlands was not glaciated and a population persisted there. The part of the range lost at this time was in the north. During post-glacial Pleistocene time, the southern half of the Scottsboro Lowlands was reoccupied as well as territory lost on the Dearborn Uplands. The present range of the species is a triangular area bounded on the south by the Ohio River, on the east by the Big Miami and Stillwater River and on the northwest by the White River (Rhoades, 1941a).

O. limosus.—This species had become established over a wide range on the coastal plains of the mid-Atlantic states. The relict population in the upper Ohio, from which the eastern population came, had been removed by glaciation, drainage changes and the invasion of its interior range by later derivations of the Cambarinae, namely, *O. propinquus*, *O. rusticus* and *C. bartoni*.

This map graphically demonstrates the wide distribution of *O. limosus* of the Atlantic drainage which has been displaced by a sequence of Pleistocene events. In contrast the endemic species of the Cumberland Plateau are minute relicts confined to small drainages which were relatively undisturbed by Pleistocene glaciation. It would seem that the greater the Pleistocene displacement the wider the present distribution of a species within the Section *limosus*.

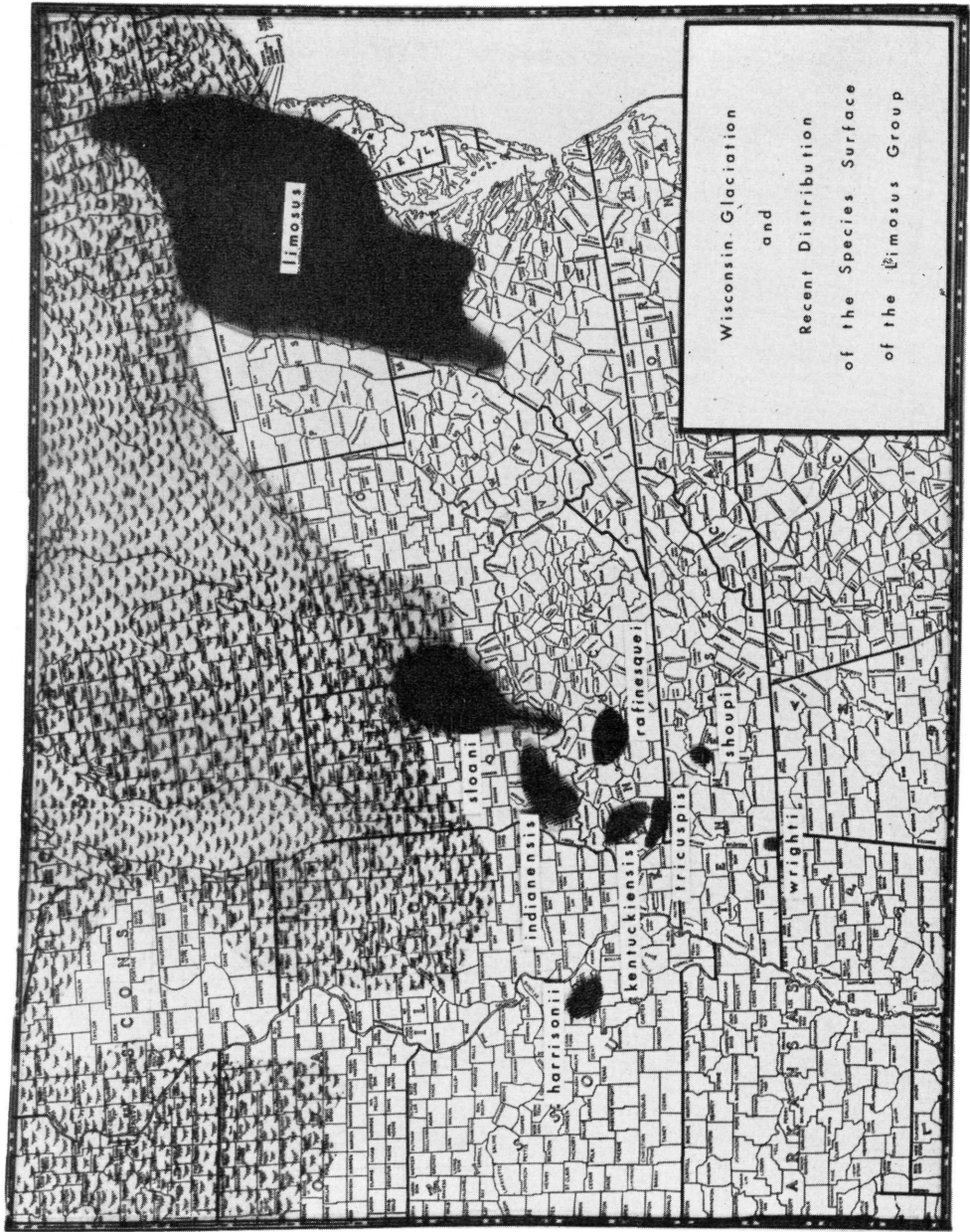


FIGURE 7

rafinesquei complex. Its development in the lower Tennessee parallels the other isolated species on the Cumberland Plateau. The northward course of the lower Tennessee has been a feature of the western plateau since late Tertiary time and received its ancestral *rafinesquei* stock in pre-Pleistocene time.

The ecological situation in which Wright (Hobbs, 1948b) found *O. wrighti* is similar to that of the habitat of *O. kentuckiensis*. Streams of Hardin County are low in gradient with sandy or gravelly bottoms and soft muddy banks. Many species of emergent aquatics line the stream margins, and crayfish generally occupy these shaded, protected areas.

6. *Orconectes pellucidus pellucidus* (Tellkamp, 1844).

County Records: *Indiana*—Crawford, Harrison, Lawrence, Orange, and Washington counties. *Kentucky*—Edmonson and Hart counties.

This is perhaps the most frequently mentioned species of crayfish in North American natural history. Many early records are inaccurate in the sense that naturalists traveling from afar labelled blind crayfish collected anywhere in western Kentucky as from Mammoth Cave. Accurate Kentucky records are known only from caves in Edmonson and Hart counties. How far its distribution extends beyond this area is difficult to ascertain. Cave habitats are difficult to explore and the general scarcity of cave crayfishes adds to the rarity with which this species has been observed in the outlying caves of Kentucky (fig. 8).

On the other hand, many zoologists have searched Indiana caverns for hypogean species, and records are more abundant from north of the Ohio River. The typical subspecies is principally in caves in the Lower Mississippian rocks under the Norman Uplands and Mitchell Plains along the backwall of the Knobstone Escarpment.

Cave habitats under the Cumberland Plateau occupied by blind crayfishes are generally streams with some resemblance of riffle and pool sequence. Cave crayfishes are principally pool dwellers. Riffle populations, so typical of epigean streams, do not form. Adults generally retreat into cavities under broken pieces of rubble. With predator pressure reduced in these stygian areas many crayfish do not respond to cover objects but merely remain quiet in the shallow margins of pools.

7. *Orconectes pellucidus inermis* Cope, 1871.

County Records: *Indiana*—Bartholomew, Brown, and Monroe counties.

This blind crayfish with reduced spines occupies the northernmost subterranean of the Cumberland labyrinth. Some of the localities collected are actually in caves under areas overrun by Kansan and Illinoian ice. The species may have spread into these passageways since Illinoian time. It may also be possible that these caverns were not collapsed and suitable habitats and a crayfish fauna persisted.

The ecological situation in which this subspecies lives is not significantly different from that of the species in the Mammoth Cave area.

8. *Orconectes pellucidus packardii* Rhoades, 1944.

County Records: *Kentucky*—McCreary and Pulaski counties.

O. pellucidus packardii is a local subspecies of the blind crayfish isolated in caves of the Cumberland Mountains in southeastern Kentucky by the deep dissection of the landscape by the Cumberland River and its tributaries. Populations seem to be small since cave owners report seeing crayfish only on rare occasions.

These caverns, perforating the massive Mississippian limestone, are relatively mud free in the upper levels, and clean sharp gravel and rubble floor the clear pools. A considerable amount of rimstone in Eureka Cave, McCreary County,



FIGURE 8. Recent distribution of the hypogean species of the Group *limosus*. The four subspecies of *O. p. pellucidus* in caves under the Cumberland Plateau are essentially isolated from one another in discontinuous subterranean passageways. The lacunae in this system are the result of entrenchment of surface streams.

retains extensive shallow pools. A part of the cave system in this area has been flooded by the formation of Kentucky Lake on the Cumberland River.

9. *Orconectes pellucidus australis* (Rhoades, 1941).

County Records: *Alabama*—Jackson and Madison counties.

The southern subspecies of the blind crayfish seems rather abundant in the well developed subterranean drainage of northern Alabama. Dr. Walter B. Jones, in outlining the ecology of Alabama caves (Rhoades, 1941b), mentions that the presence of blind crayfishes is associated with the presence of cave fishes and aquatic insects. Individuals seem to be most numerous where surface water enters caves during the wet season. Debris washed in tends to initiate the food chains. Once begun, food chains may continue among animals present. Bat guano and the molds that grow from these deposits are important sources of food for cave species.

10. *Orconectes kentuckiensis* Rhoades, 1944.

County Records: *Kentucky*—Crittenden and Union counties.

Orconectes kentuckiensis seems endemic to the Tradewater River drainage in western Kentucky. It is interesting that the headwaters of this river in Christian County Harbor a population of *O. tricusps*, another rafinesquei crayfish. The migration of *O. tricusps* from Little River, a tributary of the lower Cumberland, to the Tradewater River could easily have been accomplished in late Pleistocene time. It was then that the plateau streams were impounded by the formation of a heavy valley train in the channel of the Ohio River.

The two species have remained isolated probably as a result of ecological factors. As was pointed out above, *O. tricusps* is a species of upland gravel and rubble streams. On the other hand, *O. kentuckiensis* is a species of low-gradient, muddy and trashy streams where it is associated with *Orconectes immunis*. It was noted in the Rough River, that when conditions permitted the presence of *O. immunis*, *O. rafinesquei* did not persist. Gradient and associated factors may then keep *O. tricusps* and *O. kentuckiensis* separated.

PRESENT DISTRIBUTION AND ECOLOGY OF THE GROUP *LIMOSUS*

11. *Orconectes indianensis* (Hay, 1896).

County Records: *Indiana*—Dubois, Gibson, Orange, Pike, Spencer, Vanderburgh, and Warrick counties.

This limosus crayfish was described by Hay from Patoka, Gibson County. Subsequently, I have collected the species in the Patoka River eastward to Orange County. Furthermore, I made collections of this species in Little Pigeon River and Anderson Creek as early as June, 1943, and have taken it again in 1949, 1954, 1956 and 1959. It seems well established. I believe the species arrived in these streams as a result of faunal loss from the Patoka valley, when it became flooded by Illinoian ice.

The typical habitat in which *O. indianensis* occurs is rather high-gradient, gravel and rubble bottom streams. The type locality, which is now a channel dredged into the alluvial Wabash lowlands, is certainly not typical for the species. In four attempts I have collected only seven specimens in a mile of stream. The Patoka River at Winslow, Pike County, and Jasper, Dubois County, more closely corresponds to the type of habitat generally occupied by limosus crayfishes.

12. *Orconectes sloani* (Bundy, 1876).

County Records: *Indiana*—Bartholomew, Clark, Decatur, Fayette, Floyd, Franklin, Henry, Jackson, Jefferson, Jennings, Randolph, Ripley, Scott, Shelby, Union, Washington, and Wayne counties. *Ohio*—Butler, Darke, Hamilton, Miami, Montgomery, Preble, Shelby, and Warren counties.

Orconectes sloani is distributed over the Ordovician, Silurian, and Devonian uplands in southwestern Ohio and southeastern Indiana. Generally speaking, the range is bounded on the east by the Great Miami and Stillwater Rivers, on the north and west by the White and on the south by the Ohio River.

Over most of the broad triangle described by the courses of these rivers, *O. sloani* is associated with *O. rusticus* in the small and moderate sized streams. Most of these streams have an abundance of flagstone rubble. Under these circumstances, numerous crayfish of the two species are not keenly competitive if there is an abundance of cover material. The larger rivers, on the other hand, flow on valley trains that have been stirred to their maximum depths by ceaseless stream flow since glacial times. As a result, the boulder and rubble complements of the valley train have settled to the channel bottom, leaving only the finer and more motile fractions to cover the present stream bottom and crayfish are scarce. *O. rusticus* persists where *O. sloani* is suppressed. In recent time, pollution of the entire length of the Stillwater and Great Miami as well as the White River in Indiana has defaunated these streams repeatedly.

On the Muscatatuck Regional Slope, little of the aggregate present in the stream beds is of cover proportion, and *O. sloani* as well as *O. immunis* burrow in muddy banks. *O. sloani* particularly occupies pockets excavated in the hard granular clay.

13. *Orconectes limosus* (Rafinesque, 1817).

County Records: *Connecticut*—Middlesex County; *District of Columbia*—*Massachusetts*—Berkshire and Essex counties; *Maryland*—Allegheny, Anne Arundel, Baltimore, Carroll, Cecil, Charles, Frederick, Hartford, Montgomery, Prince George, and Washington counties; *New Jersey*—Bergen, Burlington, Camden, Gloucester, Hunterdon, Mercer, Monmouth, Morris, Passaic, Sussex, Somerset, and Warren counties; *New York*—Bronx, Broome, Columbia, Courtland, Delaware, Dutchess, Orange, Putnam, Rockland, Steuben, Sullivan, Tioga, Ulster, and Westchester counties; *Pennsylvania*—Adams, Bedford, Berks, Bucks, Center, Chester, Columbia, Cumberland, Delaware, Franklin, Lancaster, Montgomery, Northumberland, Perry, and Philadelphia counties; *Virginia*—Augusta, Fairfax, Shenandoah, and Isle of Wight counties; *West Virginia*—Morgan County. This species has been widely introduced into Europe.

Orconectes limosus, which arrived on the Atlantic slope during the height of Illinoian glaciation, is largely an inhabitant of the drainage into Chesapeake Bay and the Delaware River. In this geographic province, it ranges from the Shenandoah Valley of Virginia to western Massachusetts. This displaced species is the most widely distributed of the Group *limosus*. Having once left its original range an ecological imbalance may have been a contributory factor to dispersal. Conservation technicians who stock fish and game in new habitats are well aware of the migratory tendencies of transplanted wildlife. Were such a tendency to have continued during the full length of Sangamon time, the species could easily have populated the Chesapeake range from its invasion south through the central Appalachians. After the Wisconsin glaciation the Delaware and lower Hudson rivers were occupied by *O. limosus*.

Ortmann (1906b), Crocker (1957), and Francois (1959) have treated the ecology of the species in some detail. It is a stream and river crayfish. As Francois indicates, it is principally an inhabitant of moderate-sized flowing streams where it may be found in rubble or in weed beds. Rafinesque, in his original description, and subsequent authors have mentioned its limited burrowing habit.

SUMMARY

This paper discusses the origin, development, and Pleistocene paleogeography of the 13 species and subspecies of crayfishes belonging to the Section *limosus*

Genus *Orconectes* in eastern United States. The present inferential study is based upon 16,000 collections made over a period of 25 years.

Freshwater crayfishes of the Family Astacidae originated in Asia in the Cretaceous period and migrated across the Bering connective to North America. The Subfamily Cambarinae developed in Mexico in early Tertiary time, and the Genus *Orconectes* had its origin in the Ozarkian Highlands in the late Moicene.

The limosus stock developed in the Ozarks in the Oligocene or Pliocene epoch. Pre-Pleistocene limosus stock developed into two types. The limosus stock of the Teays River drainage had divergent tips on the gonopods. The tips of the gonopods of the rafinesquei stock of the Cumberland Plateau were recurved.

The limosus stock in the Teays River drainage was segmented by invading lobes of Pleistocene ice. The species *O. limosus* developed from a segment isolated in the upper post-Kansan Ohio River. *O. sloani* developed from a segment preserved in the southern Indiana re-entrant and *O. indianensis* was a lower Teays species surviving the Kansan and Illinoian ice within the Indiana re-entrant.

The surface stock on the Cumberland Plateau was isolated by sedimentation which changed the conditions in the lower courses of streams. The rise and dispersal of the propinquus and rusticus complexes reduced the rafinesquei crayfishes to relicts.

Hypogean species under the Cumberland Plateau developed in the late Pliocene and have subspeciated following isolation imposed by entrenchment of the surface drainage.

The Illinoian ice sheet reversed the Yarmouth Ohio River (New Martinsville River of Stout and Lamb) and flushed vestigial populations of *O. limosus* through gaps in the Appalachian barrier. Subsequent dispersal of *O. propinquus* and the Sangamon development of *O. propinquus sanborni* destroyed relicts of *O. limosus* in the interior drainage. Since Sangamon time *O. limosus* has spread from the drainage of Chesapeake Bay to the Delaware River and the lower Hudson Valley. *O. sloani* is distributed in southeastern Indiana and southwestern Ohio. *O. indianensis* occurs in streams in southwestern Indiana. *O. harrisoni* is limited to the Big River drainage in southeastern Missouri. Five species are isolated in small surface streams in western Kentucky and Tennessee. Four subspecies of blind crayfish, *Orconectes pellucidus*, occur in caves under the Cumberland Plateau.

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